SHORT COMMUNICATIONS

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AGONISTIC BEHAVIOR OF COOPER'S HAWKS

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Most Falconiformes defend breeding or hunting areas from other conspecific and heterospecific raptors (Newton 1979). Such defense behaviors may be relatively nonaggressive (e.g., posturing, flight displays; Jamieson and Seymour 1983, Bildstein and Collopy 1985), aggressive (e.g., chases, physical contact; Jamieson and Seymour 1983, Sodhi 1991, Bustamante and Hiraldo 1993, Fernández and Azkona 1994), or combinations of displays and aggression (Dawson and Mannan 1991). Most descriptions of agonistic behavior among birds of prey are for open country species (Jamieson and Seymour 1983, Bildstein and Collopy 1985, Dawson and Mannan 1991, Sodhi 1991, Fernández and Azkona 1994). This is probably due to the relative ease in making observations in open landscapes compared to forests and woodlands. For example, aside from using Great Horned Owls (*Bubo virginianus*) as lures at traps (Bloom 1987), there are few accounts of agonistic behavior among woodland raptors. The responsiveness of woodland raptors to broadcasts of conspecific and heterospecific calls (Bosakowski and Smith 1998) and a few anecdotal accounts (Meng 1951, Crannell and DeStefano 1992), however, suggest agonistic interactions may be relatively common.

As is the case for most woodland raptors, there is little information available on the behavior of Cooper's Hawks (*Accipiter cooperii*) toward conspecific and heterospecific intruders in nest areas (Meng 1951, Rosenfield and Papp 1988). The relatively open landscape of the urban environment of Tucson, Arizona, and the approachability of urban nesting Cooper's Hawks (Boal and Mannan 1999), made it possible to observe agonistic interactions between territory holders and nest-area intruders. Here, I describe agonistic behaviors of Cooper's Hawks responding to conspecific and heterospecific intruders during the prelaying and incubation portions of the breeding season.

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METHODS

These data were collected during a study of Cooper's Hawks in the greater Tucson metropolitan area (32°12′N, 110°57′W) in southeastern Arizona, 1994–96. The area encompasses approximately 70 000 ha with an estimated human population of about 800 000. Nesting Cooper's Hawks were located through standardized surveys and were being closely monitored (Boal and Mannan 1999) so the stage of the breeding cycle was known for all observations of agonistic interactions. When a nest intrusion was observed, I recorded which member(s) of the breeding pair was present, which one(s) responded to the intruder, and the age (adult or subadult) and sex of conspecific intruders. Plumage and sexual size dimorphism facilitated the visual determination of age and sex of Cooper's Hawks. Heterospecific intruders were identified to species, age, and, when possible, sex. I categorized responses as chases, or chases with strikes (e.g., chase with observed physical contact), and noted when either a resident or intruding Cooper's Hawk vocalized during an interaction.

Observations of nest area intrusions were made during the course of routine field activities (e.g., nest checks, radiotracking) so I did not calculate a rate for intrusions per time of observation. Rather, this is a compilation of observations that, taken together, may help elucidate an understanding of the defense behavior of Cooper's Hawks.

RESULTS

I observed 19 breeding season encounters between known, marked, breeding Cooper's Hawks and intruding conspecifics. Fourteen of the intrusions occurred during the pre-laying stage (73.7%), fewer occurred during the incubation stage (26.3%), and none were observed during the nestling stage. Fifteen of the 19 intrusions elicited aggressive responses by breeding Cooper's Hawks (Table 1). Both members of breeding pairs were present during 14 (73.7%) of the 19 intrusions, but both members pursued intruders on only two (14.3%) of those 14 occasions. Males were more likely to respond to conspecific intruders ($\chi^2_1 = 11.1$, $P = 0.0008$), engaging 85.7% of the intruders, whereas females engaged only 20.0%. However, sex-related differences in responsiveness of breeding Cooper's Hawks appeared to be more closely associated with the sex of the intruder (Table 1). Four-

Table 1. Incidents of aggressive response ($N = 15$) and no response ($N = 4$) by breeding Cooper's Hawks to conspecific nest area intruders during the pre-laying and incubation periods, Tucson, Arizona, 1994–96.

	PRELAYING INTRUDER			INCUBATION INTRUDER		
RESPONDING RESIDENT	♂	♀	UNK.	♂	♀	TOTAL
Aggressive response						
♂	7	1	0	3	0	11
♀	0	2	0	0	0	2
♂♀	0	1	1	0	0	2
No response						
♂	0	0	0	0	0	0
♀	0	0	0	3	0	3
♂♀	1	0	0	0	0	1

teen (73.7%) of the intruders were males (10 adult, four subadult), four were subadult females (21.0%), and one was not identified to sex or age (5.3%; Table 1). Breeding Cooper's Hawks were more likely to aggressively respond to conspecific intruders of their own sex (Fisher exact test; $P = 0.022$; Table 1). Of the 15 aggressive interactions, 10 (66.7%) intruders were chased from the nest area and five (33.3%) were physically struck by breeding Cooper's Hawks. Cooper's Hawks also tended to be silent (77%) during aggressive responses to conspecific intruders.

Two particularly physical interactions showed the degree of aggression and potential for injury that can accompany agonistic encounters between Cooper's Hawks. In one situation, an adult male chased an intruding adult male out of the nest stand and pursued it for approximately 500 m, neither bird ever flying >20 m above the ground. On three occasions during the chase the hawks faced each other while hovering and repeatedly made stabbing strikes at each other with their feet. Contact was made several times, but neither male maintained a hold on the other. In the second situation, an adult female rose up to engage a subadult female circling above the nest stand. The adult female made several passing strikes at the intruder which rolled and extended its talons toward the aggressor. The subadult was struck solidly at least three times before leaving the area.

Four of the 19 intrusions did not elicit aggressive responses (Table 1). In the first incident, a known, marked pair of Cooper's Hawks and an unbanded subadult male were perched in plain view and within 100 m of each other. The adults appeared to ignore the subadult, which flew away from the nest area after about 15 min of observation. All nestlings of the marked pair had been banded during the previous year, so the subadult could not have been their offspring. The other three occasions occurred when intruding males from adjacent territories perched in nest trees or adjacent trees while resident females were incubating. In each case, the intruding and resident males were radio tagged; telemetry indicated resident males were away from the nest areas.

One nonaggressive interaction was observed that did not include a breeding area intrusion. Rather, the incident appeared to be a border display between the known breeding females from adjacent nests. This incident involved both females approaching each other, followed by continuous circling and altitude gain near each other, but not overlapping, until both were lost from view. One of the females was observed diving back toward its nest stand a few minutes later. No evidence of aggression was observed during the encounter.

I observed 11 intrusions by other species that elicited responses by Cooper's Hawks (Table 2). Some intrusions consisted of more than one intruding individual. Males engaged intruders during seven (63.6%), females during one (9.1%), and both members during three (27.3%) of these intrusions. Although nest-area defense by Cooper's

Table 2. Incidents of aggressive response by breeding Cooper's Hawks to heterospecific nest area intruders, Tucson, Arizona, 1994–96. Number of individual intrusions followed by total number of intruding birds in parenthesis (e.g., one intrusion by Common Ravens involved two intruding ravens.

	CORA[a]	GHOW[a]	RTHA[a]	HAHA[a]	TUVU[a]
♂	1 (2)	0	3 (4)	1 (1)	2 (4)
♀	0	0	1 (1)	0	0
♂♀	0	2 (4)	1 (1)	0	0

[a] CORA = Common Raven (*Corvus corax*), GHOW = Great Horned Owl (*Bubo virginianus*), RTHA = Red-tailed Hawk (*Buteo jamaicensis*), HAHA = Harris' Hawk (*Parabuteo unicinctus*), and TUVU = Turkey Vulture (*Cathartes aura*).

Hawks was successful in most situations, Cooper's Hawks were unsuccessful twice in driving Great Horned Owls away and, in both cases, the owls usurped the Cooper's Hawk nests.

DISCUSSION

Energetic demands in the production of sperm are probably negligible in comparison to that required for the production of energy-rich eggs. This disparity has lead to suggestions that females contribute more to the reproductive effort than males, at least up to the time of fertilization (Dawkins 1976). In contrast, Beissinger (1987) suggested Snail Kite (*Rostrhamus sociabilis*) males, and Rosenfield and Bielefeldt (1991) suggested Cooper's Hawk males make greater investments in reproduction than females because they provide most of the food, do most of the nest building, and chase potential nest predators more frequently than females. I found that breeding Cooper's Hawks were more responsive to conspecific intruders of their own sex. Thus, it appears caution should be taken with using nest defense as a measure of reproductive investment. While defense against heterospecific nest intruders and predators may be a valid indication of investment, nest defense against conspecifics may be a poor measure.

Sperm competition (Birkhead 1988) and food resource competition (Temeles 1989) are two hypotheses that are not mutually exclusive and may both partially account for the high degree of nest defense by male and comparative lack of defense by female Cooper's Hawks. The majority of conspecific intrusions were by male Cooper's Hawks and occurred during the pre-laying (i.e., fertile) stage. Resident male Cooper's Hawks always drove away intruding males and resident female Cooper's Hawks engaged in conspecific nest defense only when the intruder was a female. Likewise, Meng (1951) reported the male of a breeding pair of Cooper's Hawks making repeated strikes on a captive male tethered near the nest, but the female of the pair was comparatively unresponsive. It is possible that, in order to avoid extra-pair fertilization of the female, male members of Cooper's Hawk pairs are most diligent in driving away intruding males. In contrast, female members of breeding pairs may not avoid extra-pair copulations, but may be more inclined to drive away intruding females that could compete for food resources provided by the male. For example, in this study three intruding males failed to elicit a response by the resident females when resident males were away from the nest.

Other factors may also contribute to the agonistic behavior of Cooper's Hawks. Rosenfield and Papp (1988) suspected an intruding subadult female Cooper's Hawk killed and cannibalized nestling Cooper's Hawks. If such behaviors occur, they could lead to breeding hawks defending nest areas against conspecifics in addition to other nest predators. However, in this study I never observed intruding Cooper's Hawks acting aggressively toward nestlings, and noted one example of a male Cooper's Hawk acting as a helper at one nest throughout the breeding cycle (Boal and Spaulding 2000).

It is possible that the predominance of males among intruding Cooper's Hawks was a result of sexual differences in detectability. Such an explanation suggests that some behavior(s) of male Cooper's Hawks makes them more susceptible to detection than the physically larger females. I did not observe any behaviors among intruding or resident Cooper's Hawks that led me to believe sex-related behavioral differences influenced detectability. However, stage of the nesting cycle may influence intrusion rates. While males remain mobile during the courtship and incubation periods, movements of the nesting female become necessarily more restricted to the nest area. It seems plausible that both paired and unpaired male Cooper's Hawks may invade nest areas to seek copulations with resident females. Likewise, an unpaired female may also invade a nest area seeking a potential mate. It seems unreasonable, however, that a resident paired female would as readily leave her nest area to seek extra-pair copulations. While this line of reasoning is speculative, it appears reasonable that intrusion rates would favor males.

I suggest male Cooper's Hawks may be aggressive toward intruding male conspecifics to avoid extra-pair fertilization of their mates, and that female aggression toward intruding females may be food resource related. To address agonistic behavior quantitatively among Cooper's Hawks, detailed observations at nests should be conducted. The study should include calculations of copulation rates, correspondence of copulations to prey delivery, intrusion rates, and incidences of extra-pair copulations Difficulties would include the probable low frequency of nest intrusions, the chance of observing such intrusions when they occur, and the inherent difficulty of making such observations in wooded habitat. The density of the study population and number of floaters would also influence nest intrusion rates; lower densities would likely have lower incidence of nest intrusions, and hence, lower probability of observing the intrusions. During 679 hr of observations at Merlin (*Falco columbarius*) nests, Sodhi (1991) observed only 28 conspecific nest intrusions and five extra-pair copulations/attempts. It is difficult to draw statistical significance from so few data points, yet the study was conducted under close to ideal conditions: the population was the densest ever reported for Merlins (Sodhi 1991) and was in an urban area where observations are often more easily conducted than in natural habitats Such observations are even less likely under typical conditions. Thus, a quantitative investigation of agonistic behavior of Cooper's Hawks will require a substantial time commitment in terms of nest observation and would be facilitated by a study area with a dense population, such as one of the several urban areas where the species is now known to nest.

RESÚMEN.—Examiné los patrones de respuesta de *Accipiter cooperii* en reproducción en relación a las intrusiones al área del nido producidos por individuos de la misma especie y de especies diferentes. Quince de las 19 intrusiones produjeron respuestas agresivas por parte de los gavilanes residentes. Los *Accipiter cooperii* residentes tendían a responder agresivamente a sus congeneres intrusos del mismo sexo. Los machos de los gavilanes se involucraron mas con intrusos de otras especies que las hembras. Los patrones de defensa del área del nido por parte de *Accipiter cooperii* fueron ocasionados por diferentes factores tales como la competencia de esperma, competencia de recursos y el escenario del ciclo de reproducción.

[Traducción de César Márquez]

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